**Simple individual-based models effectively represent Afrotropical forest bird movement in complex landscapes**

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**Summary**

**1.** Reliable estimates of dispersal rates between habitat patches (i.e. functional connectivity) are critical for predicting long-term effects of habitat fragmentation on population persistence. Connectivity measures are frequently derived from least cost path or graph-based approaches, despite the fact that these methods make biologically unrealistic assumptions. Individual-based models (IBMs) have been proposed as an alternative as they allow modelling movement behaviour in response to landscape resistance. However, IBMs typically require excessive data to be useful for management. Here, we test the extent to which an IBM requiring only an uncomplicated set of movement rules (the 'stochastic movement simulator', SMS) can predict animal movement behaviour in real-world landscapes.

**2.** Movement behaviour of two forest birds: the Cabanis's greenbul *Phyllastrephus cabanisi* (a forest specialist) and the white-starred robin *Pogonocichla stellata* (a habitat generalist), across an Afrotropical matrix was simulated using SMS. Predictions from SMS were evaluated against a set of detailed movement paths collected by radio-tracking homing individuals.

**3.** The SMS was capable of generating credible predictions of bird movement, although simulations were sensitive to the cost values and the movement rules specified. Model performance was generally highest when movement was simulated across low-contrasting cost surfaces and when virtual individuals were assigned low directional persistence and limited perceptual range.

**4.** The SMS better predicted movements of the habitat specialist than the habitat generalist, which highlights its potential to model functional connectivity when species movements are affected by the matrix.

**5.** *Synthesis and applications*. Modelling the dispersal process with greater biological realism is likely to be critical for improving our predictive capability regarding functional connectivity and population persistence. For more realistic models to be widely applied, it is vital that their application is not overly complicated or data demanding. Here, we show that given relatively basic understanding of a

53 species' dispersal ecology, the stochastic movement simulator represents a promising tool for
54 estimating connectivity, which can help improve the design of functional ecological networks aimed
55 at successful species conservation.

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57 Keywords: dispersal, functional connectivity, habitat fragmentation, homing experiment, perceptual
58 range, True Skill Statistic

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## Introduction

Habitat loss has been identified as one of the main factors driving the decline in biodiversity worldwide (Gibson *et al.* 2011). In the process, original habitat cover is frequently reduced to isolated remnants resulting in the spatial segregation of once continuous populations. If the size of these remnants falls below species-specific thresholds, populations are likely to go extinct due to the negative effects of declines in genetic diversity (Dixo *et al.* 2009; Agudo *et al.* 2012) and the occurrence of demographic and environmental stochastic events. An important additional factor in explaining extinction risk of populations in fragmented landscapes is the degree of landscape connectivity (i.e. the degree to which the landscape facilitates or impedes movement among habitat patches), as exchange of individuals among patches directly affects local population densities, gene flow and patch (re)colonization probabilities (Benton & Bowler 2012). Therefore, reliable connectivity estimates are central for a correct assessment of the dynamics and viability of fragmented populations and have practical applications in landscape planning and species conservation by allowing conservation managers to assess the effectiveness of management scenarios (Baguette *et al.* 2013). However, connectivity is frequently estimated by using models which oversimplify the process actually driving the loss of connectivity (Moilanen 2011).

Connectivity is driven by spatial displacement of individuals. For most animals inhabiting terrestrial fragmented landscapes, spatial displacement involves active locomotion across land-cover types comprising the intervening landscape (hereafter 'the matrix'). Empirical studies have demonstrated that movement patterns across landscapes are not random but rather reflect behavioural responses to environmental factors. Mainly by using experimental release experiments, these studies have shown that individuals may alter their movement trajectories in response to boundaries between different matrix land-cover types (Haddad 1999; Gillies & St. Clair 2010; Aben *et al.* 2012) and that permeability of boundaries may be modulated by the width of gaps (Bakker & Van Vuren 2004; Ibarra-Macias, Robinson & Gaines 2011). These matrix effects on movement behaviour can affect the

87 length of movement trajectories (Gillies & St. Clair 2008; Hadley & Betts 2009), time spent in the
88 matrix (Belisle, Desrochers & Fortin 2001; Kennedy & Marra 2010) and return success to the patch of
89 origin (Gillies & St. Clair 2008; Belisle, Desrochers & Fortin 2001). In line with these behavioural
90 observations, the degree to which patches are functionally connected is strongly determined by
91 properties of the matrix (Ferreras 2001; Revilla *et al.* 2004; Bender & Fahrig 2005). Because the rate
92 of inter-patch movement is a crucial parameter for the predictions of spatially explicit population
93 models, connectivity measures that adequately describe landscape effects on the outcome of the
94 dispersal process are needed to improve their predictive power (Revilla & Wiegand 2008).

95 However, despite the recognition that animal dispersal is driven by the complex interaction between
96 movement and external environmental factors, in the context of landscape planning and species
97 management, connectivity has hitherto almost exclusively been modelled by using simple distance-
98 based functions (Moilanen & Nieminen 2002), the least cost path (LCP, e.g. Cushman, McKelvey &
99 Schwartz 2009) or graph-theoretic methodologies (e.g. Alagador *et al.* 2012) which themselves
100 typically employ Euclidean or cost distances between patches. The assumption that displacement of
101 individuals among sites is a deterministic function of Euclidean inter-patch distance implies either
102 that the inter-patch matrix is homogenous or that animal movement is unaffected by environmental
103 heterogeneity; conversely, the assumption that animals move along optimal inter-patch linkages
104 (LCPs) implies that dispersers know the location of a target patch and are able to evaluate potential
105 routes to it (Palmer, Coulon & Travis 2011). Although these measures can be informative for the
106 purpose of corridor design on larger geographical scales (Alagador *et al.* 2012), their limitations in
107 predicting inter-patch movement rates across landscapes (i.e. functional connectivity sensu Taylor *et*
108 *al.* 1993) severely limit their use to design landscapes aimed at maximizing the persistence of focal
109 species (Baguette *et al.* 2013).

110 A potentially more realistic framework for estimating functional connectivity comprises individual-
111 based models (IBMs), as these allow explicit simulation of animal movement across realistic

landscapes (e.g. Zollner & Lima 1999; Bartoń *et al.* 2012). By incorporating correlation between movement steps and bias towards or away from different environments, IBMs can be designed to reproduce interactions between individual movement behaviour and landscape properties, which are considered important drivers of functional connectivity. However, although IBMs have been proven useful for addressing theoretical questions regarding sensitivity of connectivity predictions to variation in movement parameters (perceptual range [e.g. Pe'er & Kramer-Schadt 2008], directionality [e.g. Zollner & Lima 1999], properties of the matrix [e.g. Gustafson & Gardner 1996]), few attempts have been made to make IBMs accessible to landscape managers (but see Pe'er *et al.* 2011). A principal reason for this is the challenge of obtaining the detailed species-specific movement data typically required for parameterisation of these models (Baguette *et al.* 2013). Hence, there is a need for IBMs that allow estimating functional connectivity in the face of generally poor (empirical) knowledge of species' movement behaviour.

To address this, Palmer, Coulon & Travis (2011) recently developed a simple IBM, the 'stochastic movement simulator' (SMS). In SMS, mechanistic representation of animal movement is governed by two critical parameters controlling the degree of correlation between successive steps and the range over which landscape cost values affect movement behaviour, i.e. the perceptual range. Another advantage of SMS is that landscape effects on functional connectivity are based on the same landscape information as used by LCP models (i.e. cost values for each of the matrix elements), which can be estimated without very extensive data on animal movement (Richard & Armstrong 2010). Despite its simplicity, by translating landscape effects on animal movement at the appropriate scale (i.e. the individuals' perceptual range), SMS relaxes the unrealistic assumptions made by LCP methodologies and is therefore expected to generate more credible estimates of functional connectivity.

However, the key question remains whether such a simple model is capable of usefully describing animal movement across real-world landscapes. To test this, we validated SMS simulations with

detailed movement paths collected using radio-telemetry on two forest bird species (Cabanis's greenbul *Phyllastrephus cabanisi* and white-starred robin *Pogonocichla stellata*) in an Afrotropical matrix. As these species have been shown to differ in overall mobility at the scale of inter-patch movements (Lens *et al.* 2002; Callens *et al.* 2011) and also in their relative preference for matrix land-cover types at a finer scale (Aben *et al*. 2012), their movement paths are perfectly suited to test to what degree SMS can capture species-specific variation in movement behaviour. Because detailed movement data for spontaneously dispersing animals are generally difficult to obtain, we used experimentally induced movement data collected during a translocation experiment (Aben *et al*. 2012). Experimental releases are commonly used to study movement behaviour as a proxy for natural dispersal behaviour (e.g. Gillies & St. Clair 2010; Kennedy & Marra 2010). However, the tendency of animals to return to their territory means that movement paths were influenced by homing behaviour, and we accounted for this in our methods.

## Materials and methods

### The stochastic movement simulator

The SMS is a stochastic IBM in which virtual animals disperse from a predefined location and move independently across a gridded landscape according to simplified movement rules until they reach a habitat patch, emigrate from the landscape under study or die after a given number of steps (Palmer, Coulon & Travis 2011). Movement rules were specified using a combination of four parameters: the animal's perceptual range, its tendency to follow a correlated path (directional persistence), its tendency to move in the direction of its fragment of origin (goal bias) and the distance over which directional persistence is maintained (memory size); the original version of SMS (Palmer, Coulon &

161 Travis 2011) did not incorporate goal bias and memory size, which we added for reasons described
162 below. The chosen direction at each step was based on these parameters in combination with the
163 cost values of the cells surrounding the animals within the specified perceptual range. Code for the
164 enhanced version of SMS is available on request.

165 For each empirical movement path collected in the field (see below), we simulated 1000 individuals
166 from the corresponding release location. Movement decisions at each location (i.e. each 5 m x 5 m
167 grid cell, see below) are driven by the distribution of selection probabilities for each of the eight
168 surrounding cells. A cell's selection probability is proportional to the reciprocal of its 'effective cost',
169 which in turn is the harmonic mean of the cost values of that particular cell and its neighbouring cells
170 in an array extending to the edge of the animal's perceptual range (Palmer, Coulon & Travis 2011).
171 We set the perceptual range at 5, 10 or 20 grid cells, where the maximum value for this parameter
172 was based on the largest step lengths observed in the field (i.e. the largest distance at which
173 individuals responded to visual cues of the landscape; JA, unpublished data).

174 The tendency of animals to move in a straight line is controlled by multiplying effective costs by a
175 weighting factor, which is lowest for the neighbouring cell located in the same direction as taken in
176 the previous step and highest for the cell in the opposite direction (i.e. a 180˚ turn). The weighting is
177 controlled by the directional persistence parameter; larger values reduce the tendency for the path
178 to deviate from a straight line (Palmer, Coulon & Travis 2011). In this study we used directional
179 persistence values 2, 3 and 4.

180 If directional persistence only considers the direction of the previous step, a sharp turn
181 corresponding to a single cell can completely change an animal's direction. Although dispersing
182 animals typically have no predefined goals, and hence could be suspected to lack an intrinsic
183 motivation to move along cardinal or ordinal axes, both theoretical studies (Zollner & Lima 1999;
184 Bartoń *et al.* 2012) and empirical observations (Delgado *et al.* 2009) indicate that dispersing
185 individuals follow highly correlated paths at scales exceeding those of individual steps. To account for

this behaviour, the original model was extended by applying DP to the mean direction averaged over a number of preceding steps determined by an additional parameter (memory size; either 2, 4 or 6 steps in this study). Thus, individuals with a large memory size are more likely to resume their original movement direction after a temporary change in direction.

To control for the paths used to validate SMS simulations being influenced by homing behaviour of translocated birds, the goal bias parameter was introduced. This parameter controls the weighting of surrounding cells in relation to their deviation from the goal (i.e. the bird's capture location) in a similar way to directional persistence. We used goal bias values of 1.05, 1.1, 1.2 and 1.3, where higher values indicate a stronger tendency of the simulated individuals to move towards their capture location.

Study area and movement paths

Movement paths were collected in a montane Afrotropical landscape (Taita Hills, south-east Kenya [03°20'S, 38°15'E]; Aben *et al.* 2012), consisting of a fine-grained mosaic of human settlements, small-holder cultivation plots and indigenous forest remnants (Pellikka *et al.* 2009). Land-cover information for the study area was derived from airborne true-colour images converted to image mosaics at a spatial resolution of 0.5 m (Pellikka *et al*. 2009). The cost surface was derived from the land-cover model used by Aben *et al*. (2012); a grid of 5 m x 5 m cell size and seven land-cover types: indigenous forest, exotic plantation, agroforestry, bush, field, built-up area and road. The cell size was chosen corresponding to the accuracy of our bird observations obtained by radio-telemetry. For the purpose of this study, we created a landscape grid omitting road (replacing it by the bordering land-cover type) because it was difficult to assign a relevant cost value. This modification is unlikely to affect SMS performance in predicting actual movement paths, as Aben *et al*. (2012) showed that the amount of road intersected by actual movement steps was not different from the amount in 20 random alternative steps.

The movement data used for SMS validation were represented by detailed movement paths of two forest bird species (*P. cabanisi* [n=27] and *P. stellata* [n=21]). Both species are representative of the forest bird community of the Taita Hills but they are not equally dependent on intact indigenous forest; *P. cabanisi* exclusively occurs in indigenous forest fragments (Callens *et al.* 2011), whereas *P. stellata* also inhabits disturbed and plantation forests (Githiru, Lens & Bennun 2007). Additionally, movement of *P. cabanisi* was more affected by the matrix (Aben *et al*. 2012) and its populations showed higher genetic differentiation between three forest fragments in the Taita Hills (Callens *et al*. 2011), suggesting that higher forest dependency results in lower matrix permeability. Henceforth, based on this information, we will treat *P. cabanisi* as a forest specialist and *P. stellata* as a forest generalist.

Movement paths were generated from successive bird locations recorded during translocation experiments (see Aben *et al*. 2012 for methods and example paths). Four individuals (one *P. cabanisi* and three *P. stellata*) were discarded for the purpose of the present study, because large parts of their paths (>50% of their total length) could not be reliably documented.

Cost values

The SMS algorithm incorporates a cost surface similar to LCP (i.e. cost values are scaled relative to preferred habitat; see Adriaensen *et al.* 2003). In our study, cost values were assigned to the five matrix land-cover types to reflect their hypothesized resistance to movement relative to indigenous forest. We created seven cost surfaces with cost value of 10 for field, but different values for exotic plantation, agroforestry and bush (sets 1–7, Table 1). Also, to evaluate the sensitivity of SMS performance to differences in contrast between woody and non-woody matrix land-cover types, we created two alternative cost surfaces based on set 2, where field was assigned a cost value of 5 and 20 (set 8 and 9, respectively; Table 1). Built-up area was assigned a cost value 100 times higher than field in all cost surfaces, as this land-cover type was regarded to be invariably highly resistant to

236 movement. Finally, we created a homogeneous cost surface where all land-cover types were
237 assigned a cost value of 1 (set 0, Table 1).

238

239 Assessing IBM performance

240 Model performance was judged based on the frequency of visits to grid cells by simulated individuals
241 (henceforth "cell selection probability"). For every grid cell in each simulation we calculated this
242 probability as the proportion of simulated individuals (out of 1000) that passed through this cell at
243 least once. To evaluate the spatial fit between simulated movements and actual movement paths,
244 we compared the cell selection probabilities to the actual movement paths of birds using the True
245 Skill Statistic (TSS, Allouche, Tsoar & Kadmon 2006). The TSS ranges from - 1 to 1, where evaluation
246 values of TSS > 0.4 are considered to be indicative of good predictions (Eskildsen *et al.* 2013). The TSS
247 is an often used evaluation statistic in species distribution modelling but has also been used to
248 evaluate predictions based on dispersal simulations (La Morgia *et al.* 2011). It is based on the
249 proportion of correctly predicted presences (sensitivity, cells visited by both actual birds and
250 simulated individuals) and the proportion of correctly predicted absences (specificity, cells neither
251 visited by actual birds nor by simulated individuals). Predicted absences were only considered if a
252 particular cell could have been visited by a bird during the duration of the translocation experiment
253 (i.e. a 'true' absence). This applied to all cells that were located within an ellipse with foci on the
254 release and capture location of each bird and with an eccentricity of 0.68 (cf. Aben *et al*. 2012) and
255 that were located within a distance of the release location equalling the maximum observed distance
256 travelled during a one-day experiment (i.e. 1013 m for *P. cabanisi* and 945 m for *P. stellata*). We
257 classified each grid cell either as a predicted presence or a predicted absence according to the
258 threshold that maximized the sum of sensitivity and specificity MaxSens+Spec criteria in package
259 PresenceAbsence (Freeman 2007), and calculated the corresponding TSS (i.e. sensitivity+specificity-1;
260 Fig. 1).

In order to assess the effects of movement parameters and cost sets on the simulations, a TSS value was obtained for each combination of settings (n=108) for each cost set, and averaged over all simulated paths per species. We then used an ANOVA with TSS as the dependent variable and examined the variance explained by five main effects (i.e. cost, perceptual range, goal bias, directional persistence, memory size) and their higher-order interactions. As statistical significance in itself is relatively uninformative in the case of simulated data, we assessed the strength of the associations between TSS and the explanatory variables through the examination of partial Eta squared [$\eta_p^2$ = SSeffect / (SSeffect+SSerror);R package heplots (Fox *et al*. 2012)]. Like $R^2$, $\eta_p^2$ is a measure of effect size that is independent of the degrees of freedom used in the analyses. In addition, we assessed false positive and false negative error rates in models to interpret better the sources of prediction error.

**Results**

SMS simulations were sensitive to the movement rules specified and the cost values assigned to the landscape which profoundly influenced their accuracy in predicting the movement paths of both forest bird species (range of TSS-values obtained were 0.297–0.586 for *P. cabanisi* and 0.276–0.481 for *P. stellata*).

The five-factor ANOVA revealed four significant four-way interactions (Table 2). However, effect sizes indicated that only the interaction between goal bias, directional persistence, memory size, and the cost set used ($\eta_p^2$ 0.46 and $\eta_p^2$ 0.44 for *P. cabanisi* and *P. stellata*, respectively) and between goal bias, directional persistence, perceptual range and the cost set used ($\eta_p^2$ 0.42, *P. cabanisi* only) could be considered important.

For each species, the most important four-way interaction was examined visually by plotting the TSS for different cost sets and for each level of goal bias, memory size and directional persistence (Fig. 2).

285 The effect of goal bias on model performance differed strongly between species (Fig. 2). For *P.*
286 *cabanisi*, model performance clearly peaked when simulations were only weakly biased towards the
287 location of capture but decreased markedly when this bias increased, especially when directional
288 persistence was low and memory size small. For *P. stellata*, the effect of goal bias was only present
289 when directional persistence was low and memory size either low or moderate (Fig. 2Ba-b). For both
290 species, the effect of memory size was relatively small at low levels of directional persistence but had
291 a strong negative effect on model performance when directional persistence was high (Fig. 2g-i). The
292 combination of strong directional persistence and a large memory size resulted in the poorest SMS
293 predictions for both species (Fig. 2i).

294 The second most important four-way interaction (Fig. 3), showed that model predictions were most
295 accurate at the smallest perceptual range. At larger PRs model performance decreased. This negative
296 relationship was most pronounced at low directional persistence and for the cost set which
297 represented the strongest contrast in cost values between the woody matrix and field (i.e. set 1, Fig.
298 3). In contrast, model performance was not sensitive to variation in perceptual range when contrast
299 between land-cover types was low (i.e. set 8, Fig. 3).

300

301 Cost sets

302 Model performance was sensitive to the cost values assigned to the different matrix land-cover
303 types. In particular, performance peaked when there was a relatively low contrast between woody
304 matrix land-cover types and field (i.e. set 8) and was poorest when this contrast was strong (i.e. set
305 1). Inspection of the mean error rates in predictions showed that this was primarily attributable to
306 differences in the proportion of false negatives (i.e. actual occurrence at predicted absence) between
307 cost sets, which were lowest when contrasts were low and vice versa (Fig. 4).

Based on the *F*-values, results of the original ANOVA indicated that properties of the landscape had a larger effect on model performance for *P. cabanisi* compared to *P. stellata* (Table 2). However, differences between species in the effect size for the cost set as explanatory variable were small. To confirm this trend, we repeated the ANOVA for the cost sets which differed only in the ranking of the woody matrix land-cover types (i.e. sets 2-7). Now, the effect size for the cost set remained high for *P. cabanisi* ($\eta_p^2 = 0.964$) but dropped considerably for *P. stellata* ($\eta_p^2 = 0.696$). Within these costs sets, best predictions were obtained for set 2 and worst predictions for set 7 (based upon visual inspection of Fig. 2).

Finally, overall performance of the homogeneous cost set was relatively poor for *P. cabanisi* but relatively good for *P. stellata* (Fig. 2). This difference in performance between species was mainly attributable to the proportion of false positives (i.e. predicted presence but no actual occurrence) which was, compared to the other cost sets, highest for *P. cabanisi* and lowest for *P. stellata* (Fig. 4).

**Discussion**

Our results show that a simple IBM coupled to a cost surface is capable of predicting animal movement across heterogeneous landscapes. SMS thus represents a promising tool for translating animal–landscape interactions at the individual and local scales into higher-scale ecological and spatial patterns (e.g. estimating functional connectivity). Given the fact that accurate information on the landscape and cost surfaces are a core component of modern-day landscape and species management, SMS represents an attractive alternative to existing methods that typically rely upon Euclidean or least cost distances, often coupled with graph-theoretic methods. Moreover, IBMs such as SMS can increase (cost-)efficiency in planning conservation strategies, as they facilitate direct assessment of the functionality of structural linkages between habitat patches (e.g. the design of optimal corridors or stepping stones). For example, SMS could readily be used to determine both how frequently potential new stepping stones would likely to be used by dispersing individuals and

how the addition of new stepping stones would likely impact inter-patch transfer of individuals. In this respect, SMS can effectively be used as a stand-alone application to allow ranking of different management scenarios according to their corresponding contribution to functional connectivity between habitat patches, but it also has considerable potential to be used as a dispersal sub-model implemented in spatially-explicit population models to assess the effectiveness of alternative management interventions at the (meta)population level.

Our validation of SMS by means of detailed movement paths of two forest bird species showed that simulations were capable of usefully predicting such paths across a relatively complex matrix landscape. We previously showed (Aben *et al*. 2012) that actual bird movements were particularly sensitive to boundaries between woody matrix land-cover types and fields, resulting in stronger deviation of movement trajectories. However, given the fact that the Taita matrix is very fine-grained, birds frequently had to cross open agricultural fields in order to return to their fragment of origin. In line with these observations, the ability of SMS to describe these movements depended strongly on the way this landscape effect was incorporated in the model. In general, SMS performance was optimal when the degree of contrast between the woody matrix land-cover types and field was relatively low. Inspection of error rates in predictions between the different cost sets suggests that this relationship was predominantly driven by the ability of SMS to predict actual movements across fields; simulated birds were able to move across fields at low contrast, whereas higher contrasts prevented these particular movements. The fact that the negative effect of highly contrasting fields on model performance was largest for the generalist *P. stellata* confirms this explanation, as this species is expected to cross this land-cover type more frequently than *P. cabanisi*. In contrast to the strong effect of fields on step selection of homing birds, boundaries between the woody matrix land-cover types invoked less pronounced and consistent behavioural responses (Aben *et al*. 2012). The fact that performance of SMS was not very sensitive to the ranking

358 of these land-cover types therefore is in line with our expectation. However, besides avoidance of
359 fields, route decisions of *P. cabanisi* were also driven by composition of the woody matrix as it
360 moved in decreasing order of preference through indigenous forest, agroforestry and exotic
361 plantation/bush, whereas *P. stellata* exhibited no such behaviour (Aben *et al*. 2012). The result that
362 sensitivity of model performance to variation in the ranking of woody land-cover types was larger for
363 *P. cabanisi* indicates that SMS simulations were able to capture differences in movement behaviour
364 of a habitat specialist (whose movements are influenced by avoidance of fields and by the
365 composition of the woody matrix) and a generalist (whose movements are mainly influenced by an
366 avoidance of fields only).

367

368 Apart from the distribution of cost values, movements of virtual dispersers are affected by the
369 movement parameters of SMS. Because movements are simulated on a cell-by-cell basis, SMS does
370 not provide a perfect mechanistic description of field-derived movement rules (e.g. step lengths, turn
371 angles, c.f. Revilla *et al.* 2004). Instead, each move results in a spatial displacement determined by
372 the cell-size of the landscape grid and an angle relative to the preceding step influenced by the
373 degree of correlation specified. Hence, the ability of SMS to model species-specific movement
374 patterns across landscapes is strongly dependent on the quality of information in the cost surface.
375 Our results strongly emphasize this, not only because model fit differed markedly between cost sets
376 (see above) but also because predictive accuracy of SMS peaked when the influence of the
377 parameters governing the movement rules was minimized. As cell selection probabilities are
378 determined by their effective cost value weighted by the parameters controlling degree of
379 directional persistence and goal bias, increasing the weighting factors of these parameters overrules
380 landscape effects on simulated movements in favour of increased directionality or goal attraction.
381 Illustrative of this effect is the clear difference in sensitivity of model performance to variation in the
382 goal bias parameter between the two species; increasing the effect of homing behaviour on

simulations strongly decreased the ability of SMS to predict movements of the forest specialist *P. cabanisi* (for which movements were strongly influenced by the matrix), while no such effect was apparent for the generalist *P. stellata* (for which movements were less consistently affected by the matrix). Another example is the strong negative effect of the interaction between directional persistence and memory size on model performance for both species. A strong directional persistence in combination with a large memory size resulted in a higher proportion of false positives (data not shown) which indicate that at this combination of parameter settings, simulated individuals lose their flexibility to react to borders between land-cover types, resulting in an increase of suboptimal movements as individuals are being "pushed" into high-cost land-cover types.

In contrast to the SMS parameters discussed above, the perceptual range does not directly control movement, but modifies the scale over which cost values are assessed. Because cell selection probabilities were based on the harmonic mean of the cost values within the perceptual range, they were particularly sensitive to prevalence of low costs. For instance, Palmer, Coulon & Travis (2011) showed that an increased perceptual range resulted in a greater number of virtual dispersers reaching a target patch, primarily because they were better at locating low-cost stepping stones embedded in a high cost matrix. We found that perceptual range had little effect on predictive accuracy when matrix contrast was low, whereas model performance strongly decreased with perceptual range when contrast was strong. This negative relationship was mainly driven by an increase in the proportion of false negatives (data not shown). Our interpretation is that the enhanced detection of low-cost land-cover types by virtual dispersers reduced their use of fields in comparison with the empirical data, leading to a less accurate fit with actual movement across this land-cover type. This means that when more information is available for virtual dispersers they are increasingly capable of finding the least costly option through the matrix. The fact that this negatively affected model predictions may imply that movement decisions of actual birds were mainly driven by landscape cues perceived at relatively short distances.

## Synthesis and recommendations for application

There is considerable current interest in the degree of complexity that should be incorporated in ecological models, both in terms of models used for developing general insight and for models focussed on application (Evans *et al.* 2013). Here, we argue that intermediate complexity, represented in this case by a relatively simple IBM of animal movement, can represent an extremely promising approach for developing more effective *in silico* testing of alternative landscape management scenarios. We have provided a demonstration of how one such movement model can be parameterised using relatively straightforward data on bird movement. We have deliberately employed a simple model that has as few parameters as possible, yet overcomes key limiting assumptions (i.e. omniscience and foreknowledge of a destination) that are inherent within the methods that remain most used, but are likely to be poor representations of how dispersing individuals behave (Palmer, Coulon & Travis 2011). Additionally we have chosen to take a relatively simple approach to model validation, and we believe this is important in terms of encouraging wider application of IBMs.

Increasingly sophisticated approaches are currently being developed for the validation and inverse fitting of individual-based models, including pattern-oriented modelling (POM; e.g. Grimm *et al.* 2005) and approximate Bayesian computation (ABC; e.g. Beaumont 2010). These approaches have the worthy goal of seeking to make the optimum use of all available data for improving a model for a particular species. However, there is a clear tension between the use of validation and fitting methodologies requiring high technical expertise and the desire for ease of application to a broad number of species and landscapes. Our view is that, for IBMs to be broadly applied in management, we currently need to be pragmatic. We emphasise the need for some form of 'sanity check' of model output, and a single-criterion validation such as that used in this paper is straightforward to perform. It lacks the rigour and elegance of POM, or especially a method such as ABC, but it provides a rapid

and effective insurance that the model specified by the user is not very wrong. Here, we chose to use the True Skill Statistic for validation of model output against observed data. This is only one of many possible approaches. Another, which should not be underestimated, is straightforward visual inspection of animal movement trajectories and of simple summary data such as a distribution of dispersal distances. This can be particularly valuable when engaging with stakeholders both in terms of making best use of their knowledge and having them buy into the modelling process. For example, expert knowledge on occasional long-distance dispersal events might represent useful information to validate the model. If we are working with a species that is known to sometimes exhibit dispersal of >5 km and we never in 1000 replicates see simulated individuals disperse >2 km we might want to consider which parameters can yield at least occasional longer distance dispersal. Another stakeholder might have observed a species regularly moving along a habitat edge (e.g. woodland bordering field) yet very rarely recall having seen the species crossing an open field. This type of information can be used to help adjust parameters such that stakeholders see simulated individuals behaving in a way that they recognise. This is not formal statistical fitting, but the process can be an important way of soliciting valuable information from those who know a focal species, and can also help in increasing confidence in the modelling approach of those who need to have trust in the recommendations arising from the outputs. We believe that such stakeholder-driven model fitting will often be at least as important as formal statistical validation, both because it uses a different form of valuable information and because it engages with those who will potentially benefit from the modelling in a manner much easier for them to understand than formal statistics.

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461 **Supporting Information**

462 Additional Supporting Information may be found in the online version of this article.

463 **Fig. S1.** Interaction plots for the size of the perceptual range versus the cost set (S0-S9) at all levels of
464 goal bias.

Table 1. Cost sets used to evaluate sensitivity of SMS simulations to variation in landscape composition and contrast between land-cover types

| | Relative cost values | | | | | |
|---|---|---|---|---|---|---|
| | Indigenous forest | Exotic plantation | Agro-forestry | Bush | Field | Built-up area |
| Set 0 | 1 | 1 | 1 | 1 | 1 | 1 |
| Set 1 | 1 | 1 | 1 | 1 | 10 | 1000 |
| Set 2 | 1 | 2 | 3 | 4 | 10 | 1000 |
| Set 3 | 1 | 2 | 4 | 3 | 10 | 1000 |
| Set 4 | 1 | 3 | 2 | 4 | 10 | 1000 |
| Set 5 | 1 | 3 | 4 | 2 | 10 | 1000 |
| Set 6 | 1 | 4 | 3 | 2 | 10 | 1000 |
| Set 7 | 1 | 4 | 2 | 3 | 10 | 1000 |
| Set 8 | 1 | 2 | 3 | 4 | 5 | 500 |
| Set 9 | 1 | 2 | 3 | 4 | 20 | 1000 |

469 Table 2. ANOVA of the effects of goal bias (GB), directional persistence (DP), memory size (MS),
470 perceptual range (PR) and cost set (Cost) on the spatial agreement (TSS) between SMS simulations
471 and movement paths of two forest bird species. Significance level of *F*-tests: * $P < 0.05$, ** $P < 0.01$,
472 *** $P < 0.001$; effect sizes measured as partial Eta squared ($\eta_p^2$)

| | | *P. cabanisi* | | *P. stellata* | |
|---|---|---|---|---|---|
| | *d.f.* | *F*-value | $\eta_p^2$ | *F*-value | $\eta_p^2$ |
| Cost | 9 | 1836.7*** | 0.987 | 388.8*** | 0.942 |
| GB | 3 | 12444.5*** | 0.994 | 158.0*** | 0.687 |
| DP | 2 | 1001.6*** | 0.903 | 2407.0*** | 0.957 |
| MS | 2 | 3668.5*** | 0.971 | 2512.4*** | 0.959 |
| PR | 2 | 4673.6*** | 0.977 | 3214.9*** | 0.968 |
| Cost:GB | 27 | 72.9*** | 0.901 | 13.3*** | 0.624 |
| Cost:DP | 18 | 29.8*** | 0.713 | 76.4*** | 0.864 |
| GB:DP | 6 | 428.5*** | 0.923 | 241.1*** | 0.870 |
| Cost:MS | 18 | 29.3*** | 0.710 | 59.7*** | 0.833 |
| GB:MS | 6 | 210.0*** | 0.854 | 68.8*** | 0.656 |
| DP:MS | 4 | 858.0*** | 0.941 | 330.0*** | 0.859 |
| Cost:PR | 18 | 223.1*** | 0.949 | 90.8*** | 0.883 |
| GB:PR | 6 | 66.5*** | 0.649 | 228.5*** | 0.864 |
| DP:PR | 4 | 50.1*** | 0.481 | 42.6*** | 0.441 |
| MS:PR | 4 | 14.1*** | 0.207 | 11.6*** | 0.177 |
| Cost:GB:DP | 54 | 5.0*** | 0.554 | 6.0*** | 0.600 |
| Cost:GB:MS | 54 | 3.4*** | 0.460 | 2.8*** | 0.413 |
| Cost:DP:MS | 36 | 12.2*** | 0.670 | 11.4*** | 0.656 |
| GB:DP:MS | 12 | 10.6*** | 0.370 | 12.9*** | 0.417 |

| | | | | | |
|---|---|---|---|---|---|
| Cost:GB:PR | 54 | 2.5*** | 0.386 | 5.0*** | 0.555 |
| Cost:DP:PR | 36 | 5.6*** | 0.484 | 4.3*** | 0.418 |
| GB:DP:PR | 12 | 2.7** | 0.130 | 4.1*** | 0.184 |
| Cost:MS:PR | 36 | 2.5*** | 0.296 | 2.0** | 0.252 |
| GB:MS:PR | 12 | 1.6 | 0.080 | 4.2*** | 0.190 |
| DP:MS:PR | 8 | 3.4** | 0.112 | 4.6*** | 0.146 |
| Cost:GB:DP:MS | 108 | 1.7*** | 0.461 | 1.6** | 0.440 |
| Cost:GB:DP:PR | 108 | 1.5** | 0.422 | 1.0 | 0.329 |
| Cost:GB:MS:PR | 108 | 1.0 | 0.327 | 1.0 | 0.328 |
| Cost:DP:MS:PR | 72 | 0.6 | 0.176 | 1.0 | 0.258 |
| GB:DP:MS:PR | 24 | 1.3 | 0.126 | 1.6* | 0.154 |
| Residuals | 216 | | | | |

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Figure 1. Actual movement path overlaid over SMS simulations. Shading indicates the number of virtual individuals (out of 1000) which visited a particular landscape grid cell. In this case, a threshold of 17 individuals maximized the proportion of correctly predicted presences and the proportion of correctly predicted absences which translated into a True Skill Statistic of 0.732.

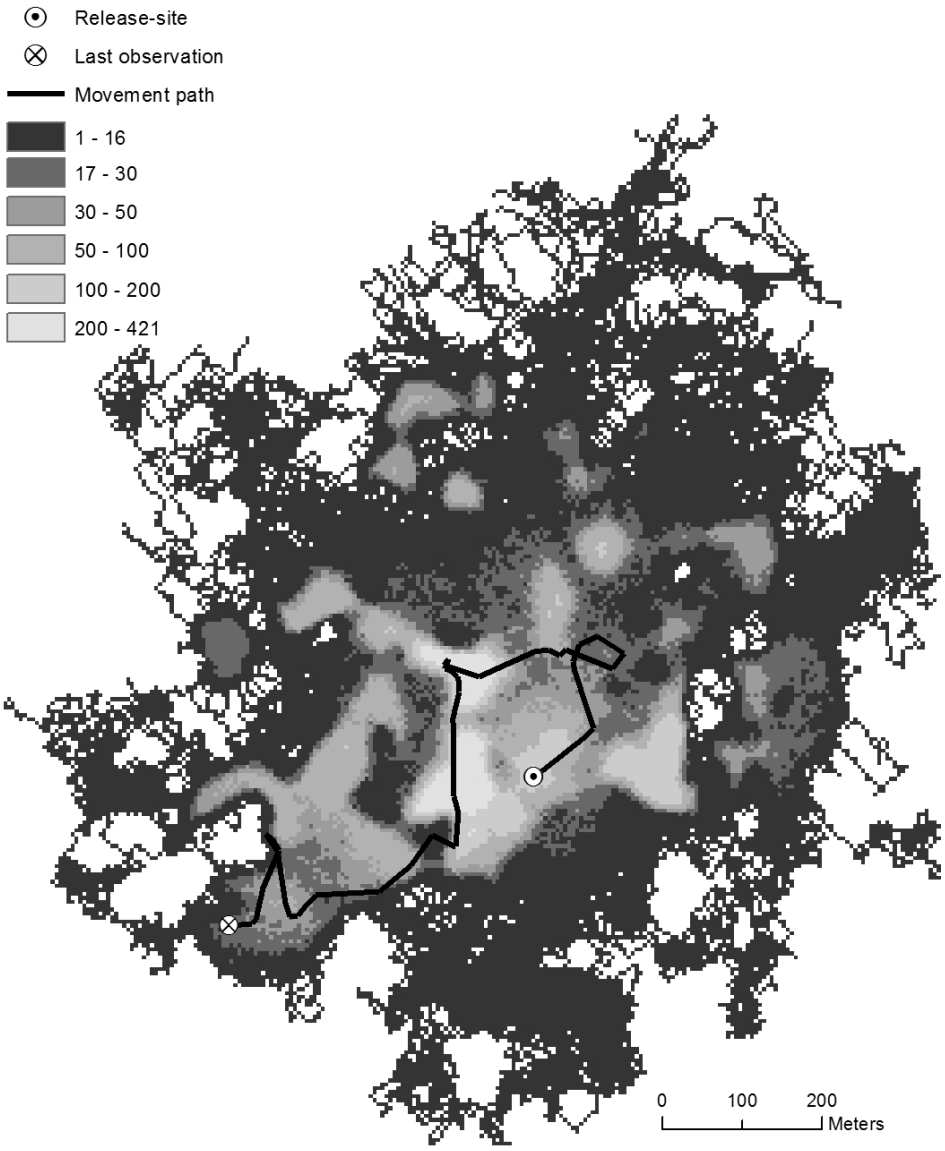
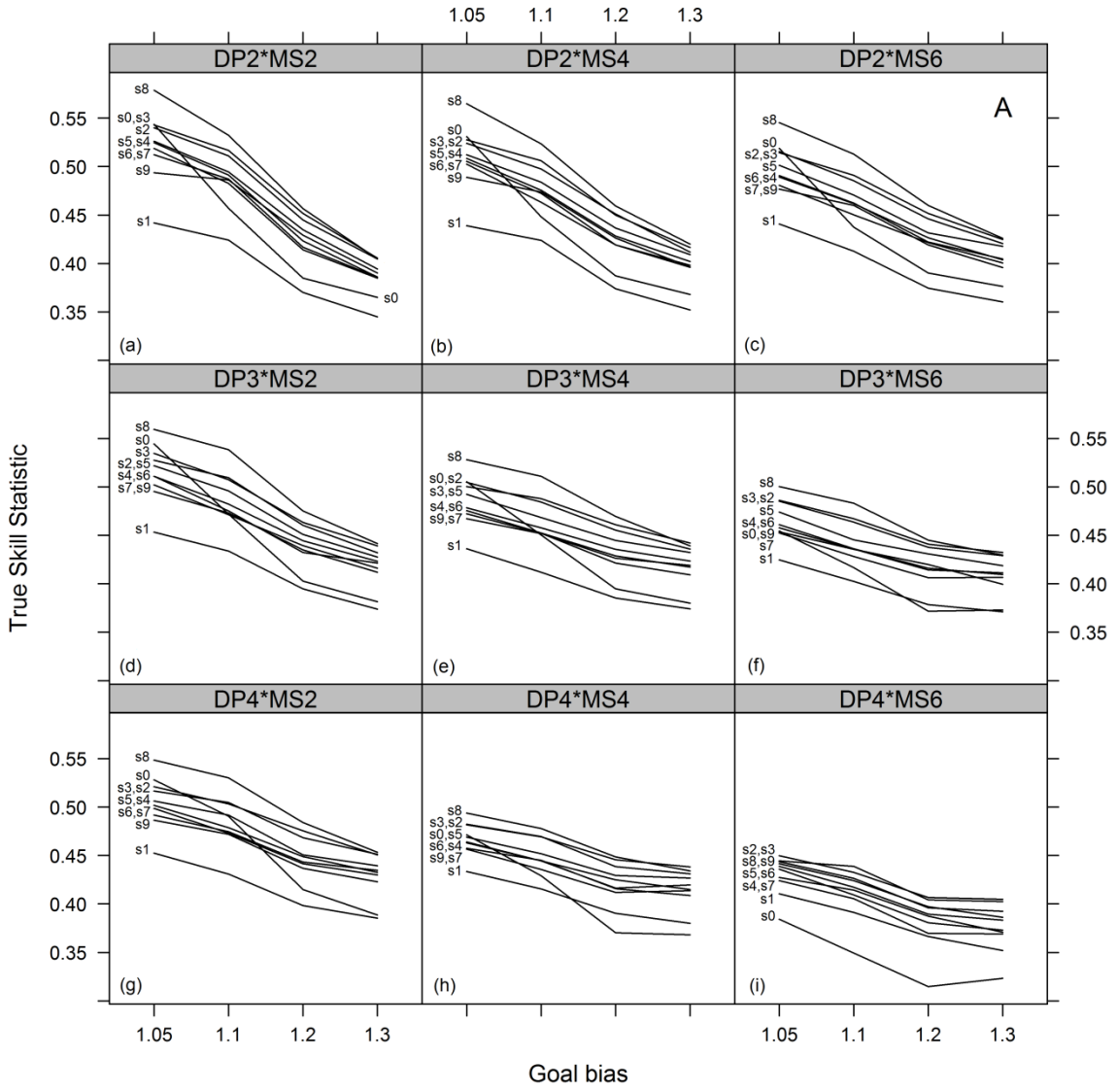


Figure 2. The effect for *P. cabanisi* (A) and *P. stellata* (B) on the True Skill Statistic of the strength of goal bias, the cost set (s0-s9), directional persistence (DP: low DP2, moderate DP3, high DP4) and memory size (MS: low MS2, moderate MS4, high MS6).



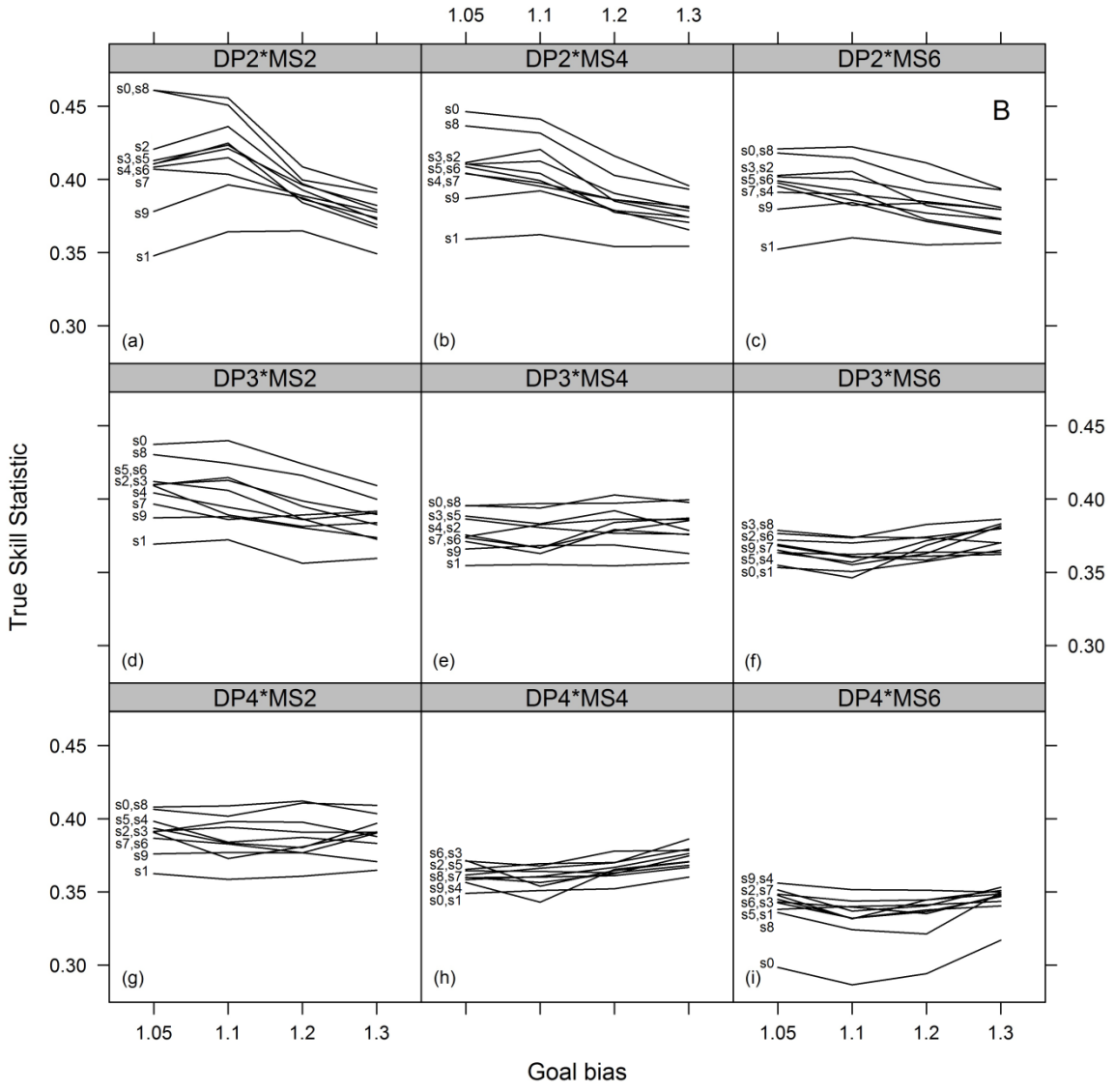

DP2*MS2
DP2*MS4
DP2*MS6
DP3*MS2
DP3*MS4
DP3*MS6
DP4*MS2
DP4*MS4
DP4*MS6
B
(a)
(b)
(c)
(d)
(e)
(f)
(g)
(h)
(i)
True Skill Statistic
Goal bias
1.05
1.1
1.2
1.3
0.45
0.40
0.35
0.30

Figure 3. The effect on true skill statistic for *P. cabanisi* of perceptual range (grid cells), the cost set (s0-s9) and directional persistence (DP: low DP2, moderate DP3, high DP4). Goal bias was constant at its lowest level (1.05) (for effects at higher levels of goal bias see Fig. S1 in Supporting Information).

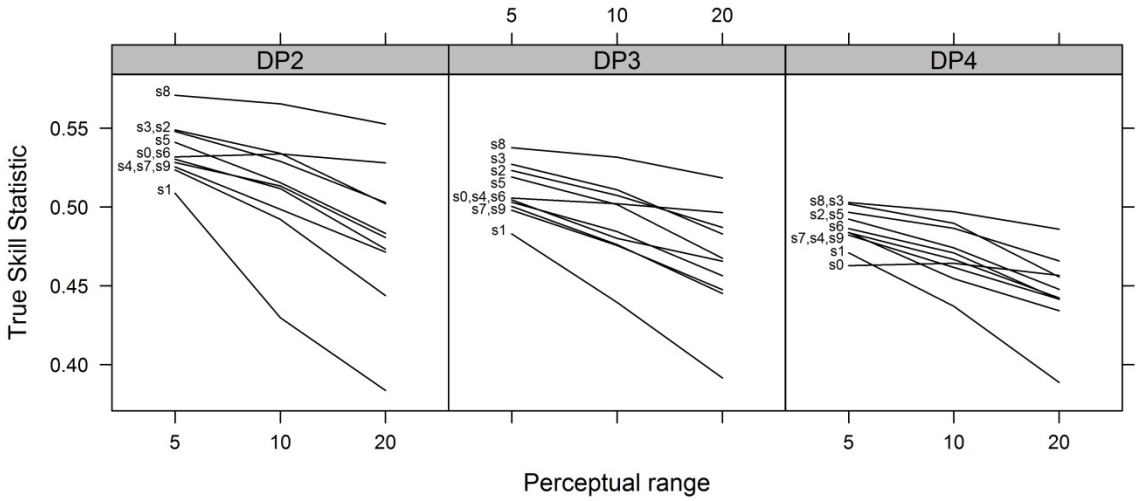
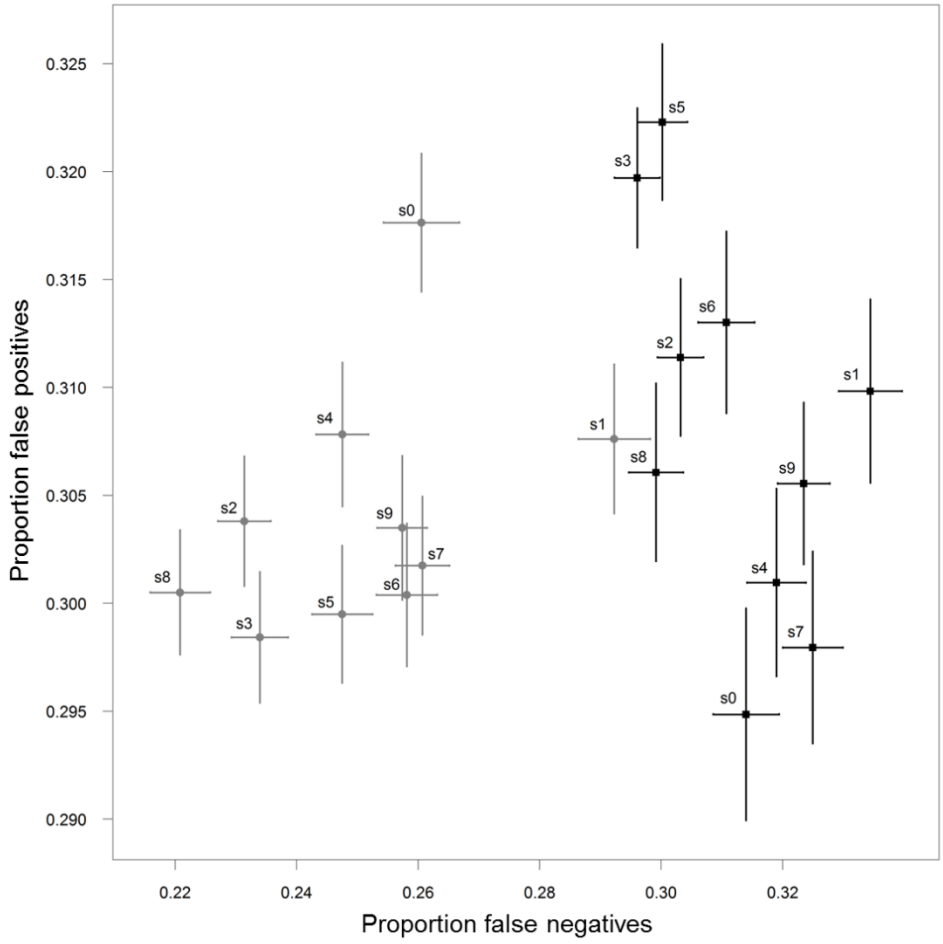


Figure 4. Average proportion of false positive and false negative errors (±SE) for each cost set (s0-s9); grey: *P. cabanisi*, black: *P. stellata*.



497 **References**


498 Aben, J., Adriaensen, F., Thijs, K.W., Pellikka, P., Siljander, M., Lens, L. & Matthysen, E. (2012) Effects
499 of matrix composition and configuration on forest bird movements in a fragmented
500 Afromontane biodiversity hotspot. *Animal Conservation,* **15,** 658-668.
501 Adriaensen, F., Chardon, J.P., De Blust, G., Swinnen, E., Villalba, S., Gulinck, H. & Matthysen, E. (2003)
502 The application of 'least-cost' modelling as a functional landscape model. *Landscape and*
503 *Urban Planning,* **64,** 233-247.
504 Agudo, R., Carrete, M., Alcaide, M., Rico, C., Hiraldo, F. & Donazar, J.A. (2012) Genetic diversity at
505 neutral and adaptive loci determines indiviudal fitness in a long-lived territorial bird.
506 *Proceedings of the Royal Society B-Biological Sciences*.
507 Alagador, D., Trivino, M., Cerdeira, J.O., Bras, R., Cabeza, M. & Araujo, M.B. (2012) Linking like with
508 like: optimising connectivity between environmentally-similar habitats. *Landscape Ecology,*
509 **27,** 291-301.
510 Allouche, O., Tsoar, A. & Kadmon, R. (2006) Assessing the accuracy of species distribution models:
511 prevalence, kappa and the true skill statistic (TSS). *Journal of Applied Ecology,* **43,** 1223-1232.
512 Baguette, M., Blanchet, S., Legrand, D., Stevens, V.M. & Turlure, C. (2013) Individual dispersal,
513 landscape connectivity and ecological networks. *Biological Reviews,* **88,** 310-326.
514 Bakker, V.J. & Van Vuren, D.H. (2004) Gap-crossing decisions by the red squirrel, a forest-dependent
515 small mammal. *Conservation Biology,* **18,** 689-697.
516 Bartoń, K.A., Hovestadt, T., Phillips, B.L. & Travis, J.M.J. (2012) Risky movement increases the rate of
517 range expansion. *Proceedings of the Royal Society B-Biological Sciences,* **279,** 1194-1202.
518 Beaumont, M.A. (2010) Approximate Bayesian Computation in Evolution and Ecology. *Annual Review*
519 *of Ecology, Evolution, and Systematics,* **41,** 379-406.
520 Belisle, M., Desrochers, A. & Fortin, M.J. (2001) Influence of forest cover on the movements of forest
521 birds: A homing experiment. *Ecology,* **82,** 1893-1904.
522 Bender, D.J. & Fahrig, L. (2005) Matrix structure obscures the relationship between interpatch
523 movement and patch size and isolation. *Ecology,* **86,** 1023-1033.
524 Benton, T.G. & Bowler, D.E. (2012) Linking dispersal to spatial dynamics. *Dispersal Ecology and*
525 *Evolution* (eds J. Clobert, M. Baguette, M. Bertzky & J.M. Bullock), pp. 251-265. Oxford
526 University Press, Oxford.
527 Callens, T., Galbusera, P., Matthysen, E., Durand, E.Y., Githiru, M., Huyghe, J.R. & Lens, L. (2011)
528 Genetic signature of population fragmentation varies with mobility in seven bird species of a
529 fragmented Kenyan cloud forest. *Molecular Ecology,* **20,** 1829-1844.
530 Cushman, S.A., McKelvey, K.S. & Schwartz, M.K. (2009) Use of Empirically Derived Source-Destination
531 Models to Map Regional Conservation Corridors. *Conservation Biology,* **23,** 368-376.
532 Delgado, M.D., Penteriani, V., Nams, V.O. & Campioni, L. (2009) Changes of movement patterns from
533 early dispersal to settlement. *Behavioral Ecology and Sociobiology,* **64,** 35-43.
534 Dixo, M., Metzger, J.P., Morgante, J.S. & Zamudio, K.R. (2009) Habitat fragmentation reduces genetic
535 diversity and connectivity among toad populations in the Brazilian Atlantic Coastal Forest.
536 *Biological Conservation,* **142,** 1560-1569.
537 Eskildsen, A., le Roux, P.C., Heikkinen, R.K., Høye, T.T., Kissling, W.D., Pöyry, J., Wisz, M.S. & Luoto, M.
538 (2013) Testing species distribution models across space and time: high latitude butterflies
539 and recent warming. *Global Ecology and Biogeography,* **22,** 1293-1303.
540 Evans, M.R., Grimm, V., Johst, K., Knuuttila, T., de Langhe, R., Lessells, C.M., Merz, M., O Malley,
541 M.A., Orzack, S.H., Weisberg, M., Wilkinson, D.J., Wolkenhauer, O. & Benton, T.G. (2013) Do
542 simple models lead to generality in ecology? *Trends in Ecology & Evolution,* **28,** 578- 583.
543 Evans *et al*. (2013) Predictive systems ecology. *Proceedings of the Royal Society B-Biological Sciences,*
544 **22,** 1471-2954.
545 Ferreras, P. (2001) Landscape structure and asymmetrical inter-patch connectivity in a
546 metapopulation of the endangered Iberian lynx. *Biological Conservation,* **100,** 125-136.

Gibson, L., Lee, T.M., Koh, L.P., Brook, B.W., Gardner, T.A., Barlow, J., Peres, C.A., Bradshaw, C.J.A., Laurance, W.F., Lovejoy, T.E. & Sodhi, N.S. (2011) Primary forests are irreplaceable for sustaining tropical biodiversity. *Nature,* **478,** 378-381.

Gillies, C.S. & St. Clair, C.C. (2008) Riparian corridors enhance movement of a forest specialist bird in fragmented tropical forest. *Proceedings of the National Academy of Sciences of the United States of America,* **105,** 19774-19779.

Gillies, C.S. & St. Clair, C.C. (2010) Functional responses in habitat selection by tropical birds moving through fragmented forest. *Journal of Applied Ecology,* **47,** 182-190.

Githiru, M., Lens, L. & Bennun, L. (2007) Ranging behaviour and habitat use by an Afrotropical songbird in a fragmented landscape. *African Journal of Ecology,* **45,** 581-589.

Grimm, V., Revilla, E., Berger, U., Jeltsch, F., Mooij, W.M., Railsback, S.F., Thulke, H.-H., Weiner, J., Wiegand, T. & DeAngelis, D.L. (2005) Pattern-Oriented Modeling of Agent-Based Complex Systems: Lessons from Ecology. *Science,* **310,** 987-991.

Gustafson, E.J. & Gardner, R.H. (1996) The effect of landscape heterogeneity on the probability of patch colonization. *Ecology,* **77,** 94-107.

Haddad, N.M. (1999) Corridor and distance effects on interpatch movements: A landscape experiment with butterflies. *Ecological Applications,* **9,** 612-622.

Hadley, A.S. & Betts, M.G. (2009) Tropical deforestation alters hummingbird movement patterns. *Biology Letters,* **5,** 207-210.

Ibarra-Macias, A., Robinson, W.D. & Gaines, M.S. (2011) Experimental evaluation of bird movements in a fragmented Neotropical landscape. *Biological Conservation,* **144,** 703-712.

Kennedy, C.M. & Marra, P.P. (2010) Matrix mediates avian movements in tropical forested landscapes: Inference from experimental translocations. *Biological Conservation,* **143,** 2136-2145.

La Morgia, V., Malenotti, E., Badino, G. & Bona, F. (2011) Where do we go from here? Dispersal simulations shed light on the role of landscape structure in determining animal redistribution after reintroduction. *Landscape Ecology,* **26,** 969-981.

Lens, L., Van Dongen, S., Norris, K., Githiru, M. & Matthysen, E. (2002) Avian persistence in fragmented rainforest. *Science,* **298,** 1236-1238.

Moilanen, A. (2011) On the limitations of graph-theoretic connectivity in spatial ecology and conservation. *Journal of Applied Ecology,* **48,** 1543-1547.

Moilanen, A. & Nieminen, M. (2002) Simple connectivity measures in spatial ecology. *Ecology,* **83,** 1131-1145.

Palmer, S.C.F., Coulon, A. & Travis, J.M.J. (2011) Introducing a 'stochastic movement simulator' for estimating habitat connectivity. *Methods in Ecology and Evolution,* **2,** 258-268.

Pe'er, G., Henle, K., Dislich, C. & Frank, K. (2011) Breaking Functional Connectivity into Components: A Novel Approach Using an Individual-Based Model, and First Outcomes. *PLoS ONE,* **6**.

Pe'er, G. & Kramer-Schadt, S. (2008) Incorporating the perceptual range of animals into connectivity models. *Ecological Modelling,* **213,** 73-85.

Pellikka, P.K.E., Lotjonen, M., Siljander, M. & Lens, L. (2009) Airborne remote sensing of spatiotemporal change (1955-2004) in indigenous and exotic forest cover in the Taita Hills, Kenya. *International Journal of Applied Earth Observation and Geoinformation,* **11,** 221-232.

Revilla, E. & Wiegand, T. (2008) Individual movement behavior, matrix heterogeneity, and the dynamics of spatially structured populations. *Proceedings of the National Academy of Sciences of the United States of America,* **105,** 19120-19125.

Revilla, E., Wiegand, T., Palomares, F., Ferreras, P. & Delibes, M. (2004) Effects of matrix heterogeneity on animal dispersal: From individual behavior to metapopulation-level parameters. *American Naturalist,* **164,** E130-E153.

Richard, Y. & Armstrong, D.P. (2010) Cost distance modelling of landscape connectivity and gap-crossing ability using radio-tracking data. *Journal of Applied Ecology,* **47,** 603-610.

Taylor, P.D., Fahrig, L., Henein, K. & Merriam, G. (1993) Connectivity is a vital element of landscape structure. *Oikos,* **68,** 571-573.

599 Zollner, P.A. & Lima, S.L. (1999) Search strategies for landscape-level interpatch movements. *Ecology,*
600 **80,** 1019-1030.
601